

NEW CROCODYLIANS FROM THE LATE OLIGOCENE WHITE HUNTER SITE, RIVERSLEIGH, NORTHWESTERN QUEENSLAND

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Four new species of crocodylian are identified from the late Oligocene White Hunter Site, Riversleigh, northwestern Queensland, one of which is also found in other System A sites at Riversleigh. All four species are assigned to known genera and some revision of two generic diagnoses is required. Two different forms of posterior cranium are also identified from White Hunter Site and retained in open nomenclature. Palaeoecological significance of four crocodylians in a single site are interpreted as a sympatric assemblage because they have different head shapes. However, the diversity in these crocodylians could also suggest a thanatocenosis involving taxa from different hydrodynamic regimes with differing degrees of forest canopy cover. □ *Riversleigh, Baru, Quinkana, Mekosuchus*, Oligocene.

Paul Michael Arthur Willis, *Quinkana Pty Ltd, 3 Wanda Cres., Berowra Hts, NSW, 2082; received 4 November 1996.*

The fossil assemblage from White Hunter Site at Riversleigh, NW Queensland contains skull fragments and postcranial material of crocodylians and other vertebrates. The fragments represent at least 4 crocodylian species. Three different maxillae are assigned to new species of known genera. Of 4 mandibles identified 3 are assigned to 3 of the species identified by maxillae; the fourth belongs to a species better known from Riversleigh's D, Sticky Beak and Pancake Sites (Willis et al., 1990). Cranial material is described but not assigned to any of the 4 new species.

Mekosuchus Balouet & Buffetaut, 1987 and *Baru* Willis et al., 1990 were previously monotypic and their generic diagnoses require revision in the light of new species assigned below. *Quinkana* was revised by Willis & Mackness (1996) and their expanded generic diagnosis (based on Molnar, 1981) encompasses the new species described here.

Mekosuchus was known from Recent cave deposits in New Caledonia. It has a unique autapomorphy: the maxilla participating in the orbit. *M. whitehunterensis* sp. nov. is the first pre-Pleistocene record of this genus.

Quinkana has 3 species: *Q. fortirostrum* Molnar, 1981 from E Queensland; *Q. timara* Megirian, 1994 is more slender-snouted from late middle Miocene of Bullock Creek, NT; and *Q. babarra* Willis & Mackness, 1996 is from early Pliocene at Allingham Creek, Queensland. *Quinkana* is distinguished by a suite of ziphodont features and is unique among mekosuchines (*sensu* Willis et al., 1993) in being a broad-snouted ziphodont. *Quinkana meboldi* sp. nov. is

the third pre-Pliocene record after *Q. timara* and a species from the late Miocene Ongeva Local Fauna, Alcoota, NT (Murray & Megirian, 1992; Murray et al., 1993; Megirian, 1993).

Baru darrowi (Willis et al., 1990) was described from middle Miocene of Bullock Creek, NT and Site D, Riversleigh. Two species of *Baru* (Willis et al., 1990) are recognised from White Hunter Site. One species is particularly small for the genus and the other species is based on material from a number of Riversleigh's System A sites (*sensu* Archer et al., 1989), including White Hunter Site. Some of the material assigned here to the second species of *Baru* was previously assigned to *B. darrowi*. *Baru* species are broad, moderately deep-snouted mekosuchines with moderately compressed teeth and a distinctive ridge on the posterior of the maxilla and the jugal.

Mekosuchus, *Quinkana* and *Baru* can all be shown to be mekosuchines. A more detailed phylogenetic analysis of these three genera forms part of a more comprehensive investigation of the phylogeny of mekosuchines (Salisbury & Willis, 1996).

The ecological implications of four crocodylians in the same deposit invites an investigation of the possible structure of crocodylian faunas. There would appear to be no ecological conflict between the sympatric existence of all four species because their different morphologies suggest the exploitation of different habitats. This is consistent with modern analogies such as some parts of the Amazon River Basin and with other fossil deposits such as Messel and Geisaltal in Germany, the Bridger Basin in the U.S.A. and the La

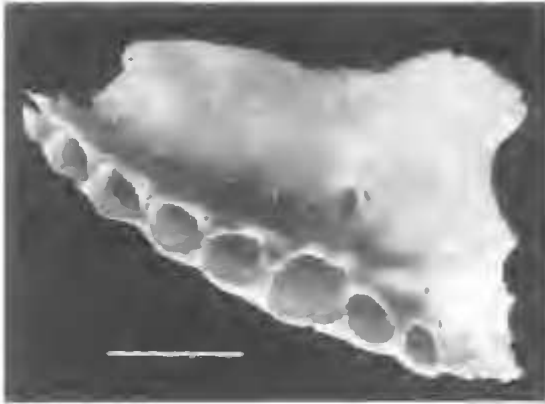


FIG. 1. *Mekosuchus whitehunterensis* n.sp., QMF31051, holotype, right maxilla, ventral view. Scale = 5mm.

Venta fauna in Colombia. Alternatively, the different crocodylians in White Hunter Site may be from different habitats and have been collected together in a thanatocenosis.

This publication was the content of a seminar presented at the Conference on Australia Vertebrate Evolution, Palaeontology and Evolution (CAVEPS) in Alice Springs, March, 1991 and published as an abstract (Willis, 1992).

Mekosuchus Balouet & Buffetaut, 1987

TYPE SPECIES. *Mekosuchus inexpectatus* Balouet & Buffetaut, 1987.

DIAGNOSIS (translated from French). Eusuchians with choanae relatively little displaced posteriorly; wings of pterygoids strongly developed posteriorly; skull deck very broad; maxilla participating in lower border of the orbit; external nares opening to the side and the front (anterolaterally); nasals not reaching external nares; palatines very narrow in their posterior part; quadratojugal lacking a spine; snout short and



FIG. 2. *Mekosuchus whitehunterensis*, QMF31051, holotype, right maxilla. Dorsal view with white arrow showing portion of the maxilla that participates in the orbit. Scale = 2mm.

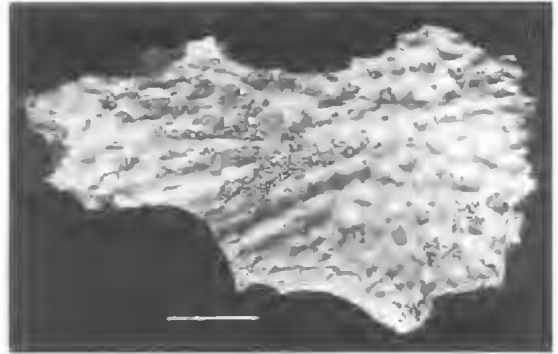


FIG. 3. *Mekosuchus whitehunterensis*, QMF31052, partial frontal, dorsal view. Scale = 5mm.

deep; splenial does not participate in the mandibular symphysis; posterior crushing teeth; 13 mandibular teeth; lower teeth occlude medial to upper series; vertebrae procoelous with strong neural spines in the cervical region; limb bones showing strong muscle insertions; presence of dorsal scutes.

My diagnosis includes the following features (apomorphies indicated by 'a') are: 1, (a) maxilla participating in lower border of the orbit. 2, snout short and deep. 3, (a) no conspicuous gap between the sixth and seventh maxillary alveoli. 4, high, narrow alveolar process. 5, symphyseal region very shallow dorsoventrally. 6, splenial anterior to the level of the seventh dentary alveolus. 7, external mandibular fenestrae strongly reduced. 8, (a) out-turned flange on the angular and surangular.

The type species diagnosis is: palatal fenestrae reaching anteriorly to the level of the sixth maxillary alveoli; posterior teeth of rounded, crushing form; symphysis reaching posteriorly to the level of the seventh dentary alveoli.

Some features of the original diagnosis are synapomorphies of wider groups and others are of uncertain value so they are not employed herein.

The character 'nasals not reaching external nares' is equivocal on available material so is not employed pending more complete material.

Mekosuchus whitehunterensis sp. nov. (Figs 1-5)

MATERIAL. Holotype, QMF31051, right maxilla (Figs 1, 2). Paratypes QMF31052, partial frontal; QMF31053, almost complete mandible; QMF31054 and QMF31055, anterior portions of dentaries. All from late Oligocene White Hunter Site, Riversleigh.

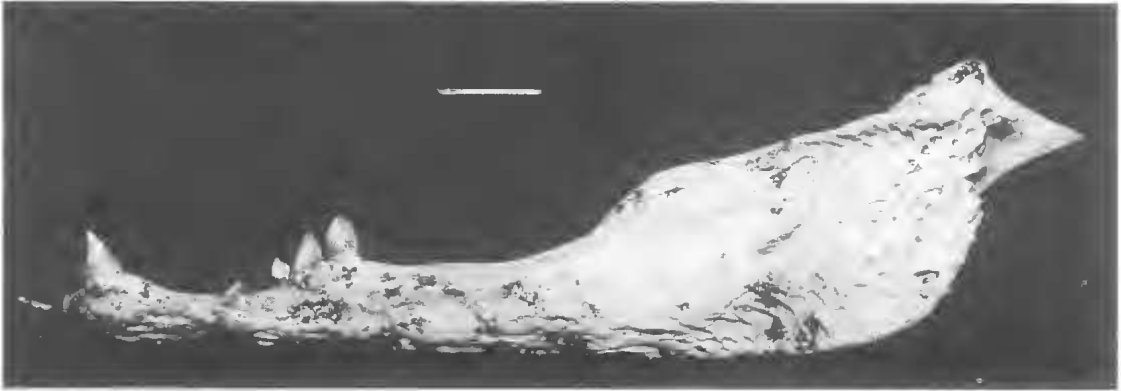


FIG. 4. *Mekosuchus whitehunterensis*, QMF31053, left mandible, lateral view. Scale = 1cm.

DIAGNOSIS. Longitudinal sulcus below the orbit; palatal fenestrae reaching anteriorly to the level of the seventh maxillary alveoli; posterior teeth compressed and blade-like; and symphysis extending posteriorly to the level of the sixth dentary alveoli.

ETYMOLOGY. From White Hunter Site.

DESCRIPTION. Maxilla broad, deep-snouted, with moderately high, narrow alveolar process (*sensu* Molnar, 1981). Lateral wall steeply in-

clined to the palate, with longitudinal sulcus ventral to the orbit. Small portion of the maxilla participating in the orbit, separating lacrimal from jugal. (Full extent to which the maxilla participated in the orbit cannot be deduced because the posterior portion is missing in this specimen.). Alveoli ovate, slightly compressed laterally, close to each other so excluding the lower series from resting between them; fifth alveolus largest; first and seventh alveoli small-



FIG. 5. *Mekosuchus whitehunterensis*, QMF31053, left mandible, dorsal view. Scale = 1cm.

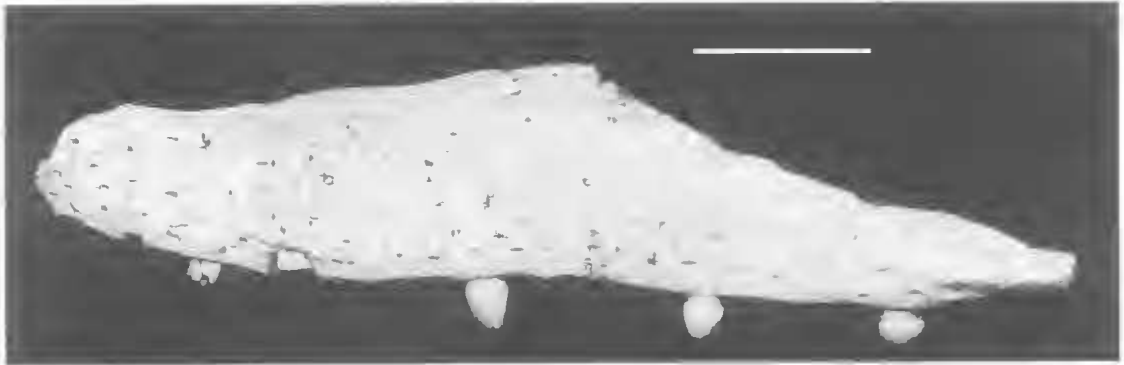


FIG. 6. *Quinkana meboldi* n. sp., QMF31056, holotype, left maxilla, lateral view. Scale = 1 cm.

est, almost equal in size. Only two pits for reception of dentary teeth medial to the upper alveoli, between the sixth and seventh alveoli, and a disproportionately large pit posterior and medial to the seventh alveolus. Palatal fenestra reaching level of the seventh alveolus.

Frontal. Closely resembles frontals of *M. inexpectatus*, very wide between the orbits; orbit margins raised, giving a concave transverse section to the dorsal surface. *crania cristae frontalis* shallow, close together leaving a wide, thin shelf between them and the orbit margins.

Mandible and dentary fragments. Pseudoheterodont with an undulating tooth row; tooth row shorter with respect to the whole mandible than in other crocodyles. Posteriorly, dentary strongly compressed laterally and deep dorsoventrally. Dentary thick around the base of each alveolus; buttressing variable in proportion to size of alveolus, not strongly developed. Slight ridge defining a groove lateral to the 12th through to the 16th alveoli probably received posterior maxillary

teeth. Splenial extending anteriorly to 7th alveolus; symphysis extending to 6th. Low ridge on the external surface of both dentaries running from below the 8th dentary alveolus onto the angular, probably strengthened the dentary. Teeth 16, with unserrated anterior and posterior carinae, becoming laterally compressed posteriorly so that posterior teeth are blade-like.

QMF31053 with large, out-turned flange on the posterior and ventral margins of angular and out-turned flange on the dorsal margin of the external surface of the surangular; flanges joining at the posterior margin of the mandible, marking boundary between the sculptured surfaces and the smoother surfaces for muscle attachment.

Articular broad, expanded medially; articular portion of retroarticular process shallowly concave. Retroarticular process short and steeply inclined. Medial side of condylar surface reduced, strongly buttressed ventrally. External mandibular fenestra reduced, almost closed. Sculpture of indistinct scarring on the external

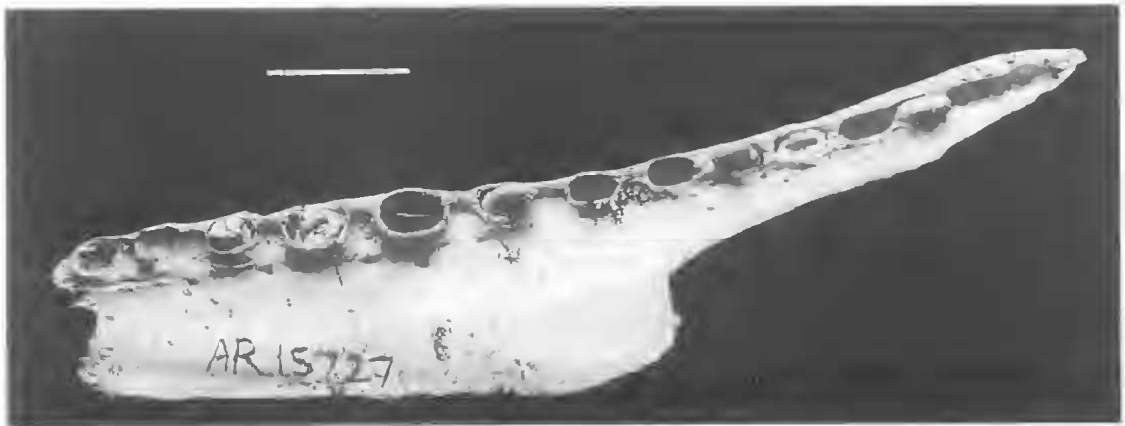


FIG. 7. *Quinkana meboldi* n. sp., QMF31056, holotype, left maxilla, ventral view. Scale = 1 cm.

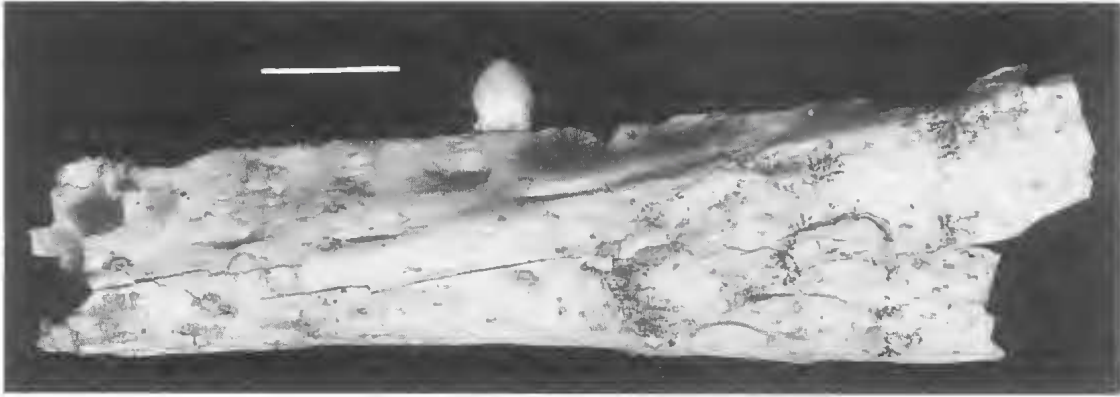


FIG. 8. Left dentary of *Quinkana meboldi* (QMF31059). Lateral view. scale = 1cm.

surfaces of the dentary and a well-developed mosaic of pits on the angular and surangular.

DISCUSSION. This mandible is very derived and shows distinct similarities to *M. inexpectatus*. Both are distinguished by: external fenestra reduced or closed; anterior edge of surangular forming distinct step dorsal to the dentary; angular and surangular flange; posterior portion proportionally short and deep; symphysis very shallow; similar sculpture. Maxillae of *M. inexpectatus* and *M. whitehunterensis* exhibit the apomorphic condition of contacting the orbit. Thus, it is most parsimonious to associate the derived mandible and maxilla from White Hunter Site, both of which most closely resemble *M. inexpectatus*. The association of mandibles and maxillae of *M. inexpectatus* is not in doubt (Balouet pers. comm.).

Quinkana Molnar, 1981

TYPE SPECIES. *Quinkana fortirostrum* Molnar, 1981

DIAGNOSIS. See Willis & Mackness (1996).

Quinkana meboldi sp. nov. (Figs 6-9)

MATERIAL. Holotype QMF31056, left maxilla (Figs 6, 7). Paratypes QMF31057, almost complete left maxilla; QMF31058, right maxillary fragment; QMF31059, dentary fragment. All from late Oligocene White Hunter Site, Riversleigh.

DIAGNOSIS. Small to moderate-sized, with 14 maxillary alveoli; palatal fenestra extending anteriorly to the level of the 8th maxillary alveolus; teeth partially interlock; snout narrower than in *Q. fortirostrum*; mild festooning; carinae of teeth without serrations.

ETYMOLOGY. For Ulrich Mebold, Max Plank Institut für Radioastronomie.

DESCRIPTION. Maxilla. Teeth 14, compressed and blade-like with anterior and posterior carinae. Alveoli compressed to varying degrees; anterior 6 teeth directed slightly posteriorly.

Alveolar ridge low, mildly undulating, uninterrupted laterally but medial side interrupted by pits for the reception of dentary teeth. Palatal fenestra extending anteriorly to the 8th alveolus. Midline palatal suture straight to the level of the 7th alveolus, then diverting laterally to accommodate a short, pointed anterior palatal process.

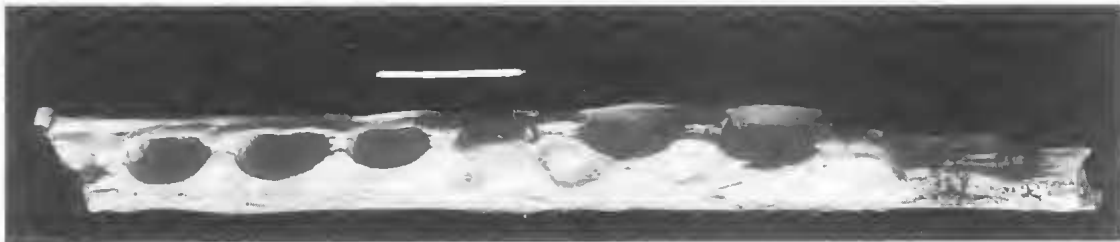


FIG. 9. *Quinkana meboldi*, QMF31059, left dentary, dorsal view. Scale = 1cm.

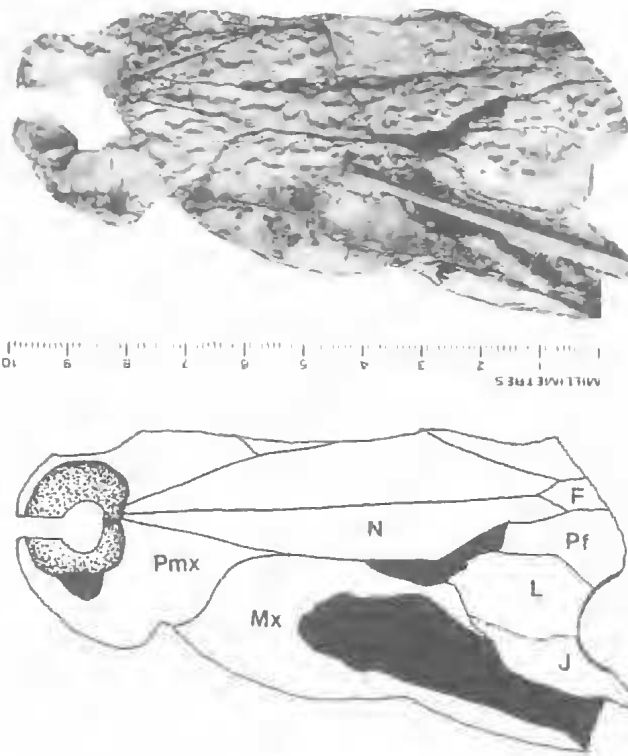


FIG. 10. *Baru huberi*, QMF31060, holotype, snout, dorsal view, with line interpretation. F=frontal; J=jugal; L=lacrimal; Mx=maxilla; N=nasal; Pf=prefrontal; Pmx=premaxilla. Scale in cm.

Dorsal surface steep-sided, indicating a deep, moderately broad snout. Preorbital or lacrimal ridge giving the snout a trapezoidal cross section anterior to the orbits. Margins contacting nasals straight. Sculpture of distinct pits anteriorly, degenerating to pitted scars posteriorly.

Alveoli with a sharply defined groove running medial to the alveoli. This appears to have been derived from the line of foramina normally found in other crocodylians in a homologous position.

DISCUSSION. The lateral compression of both the dentary and the dentition as well as the lack of festooning indicates that the dentary fragment (QMF31059) belongs to *Q. meboldi*. The single tooth is identical to the posterior teeth of QMF31056. This dentary form differs from *M. whitehunterensis* in which the posterior-most alveoli are interconnected. It also differs from dentaries attributed to *Baru* which lacks strongly

compressed alveoli and does not have a laterally compressed mandibular body.

Baru Willis, Murray & Megirian, 1990

TYPE SPECIES. *Baru darrowi* Willis et al., 1990.

DIAGNOSIS. Broad, moderately deep snout; reduction of the second premaxillary tooth during growth sometimes resulting in four premaxillary teeth in adults; premaxillary and anterior six maxillary teeth directed posteriorly; tooth crowns moderately compressed laterally; tooth crown and socket dimensions highly differentiated along both upper and lower tooth rows with correspondingly wide, deep alveolar processes; conspicuous maxillary reception pits corresponding to dentary tooth crowns situated medial to the upper tooth row; anterior margins of the palatal fenestrae extending to the level of the seventh maxillary tooth; anterior palatine process absent; splenial terminates anteriorly at the level of the seventh dentary tooth and does not enter

symphysis; external nares terminal and broadly 'apple'-shaped; distinctive bony crest arches posteriorly from the maxillae and jugals, extending to the quadratojugals.

REMARKS. The 2 new species are most closely related to Miocene *B. darrowi* from the NT (Willis et al., 1990). Some of the material attributed here to *B. wickeni* sp. nov. was previously referred to *B. darrowi*. 'Internal nares with raised rim' was included in the original diagnosis of *Baru* but its status is now uncertain.

Baru darrowi Willis, Murray & Megirian, 1990

DIAGNOSIS. Snout broad, deep; rounded premaxillae; 13 maxillary teeth; nasals excluded from external nares; anterior termination of nasal

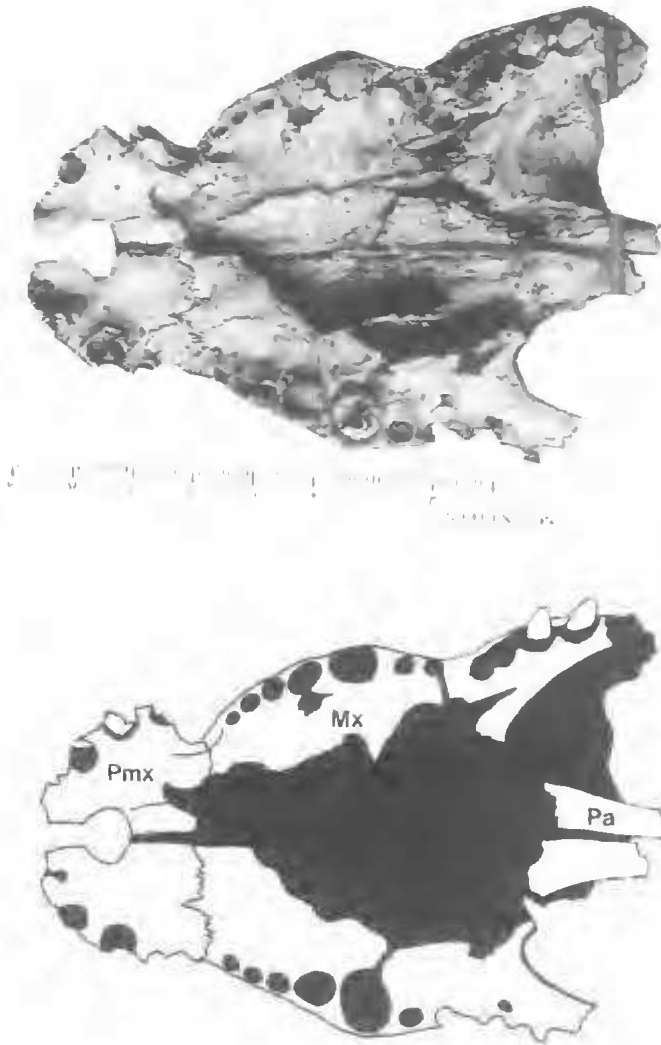


FIG. 11. *Baru huberi*, QMF31060, holotype, snout, ventral view, with line interpretation. Mx=maxilla; Pa=palatine; Pmx=premaxilla. Scale in cm.

is a short, broad wedge; serrated carinae; mandibular symphysis extends posteriorly to between the sixth and seventh dentary teeth.

***Baru huberi* sp. nov.**
(Figs 10, 11)

HOLOTYPE. QMF31060, fragmentary snout (Figs 10, 11). **PARATYPES** QMF31061, right premaxilla and anterior portion of right maxilla; QMF31062, relatively complete premaxilla; QMF31063, partial maxilla; QMF31064, maxillary fragment; QMF31065, maxil-

lary fragment; QMF31066, maxillary fragment; QMF31067, dentary; QMF31068, dentary; and QMF31069, pair of dentaries with splenic fragments. All from late Oligocene White Hunter Site, Riversleigh.

DIAGNOSIS. Snout broad, not as deep as in other species; rounded premaxillae; 14 maxillary teeth; nasals contact external nares; lateral border of the nasals without angulation at the maxilla-premaxilla boundary; non-serrated carinae; mandibular symphysis extending posteriorly to the 5th dentary teeth.

ETYMOLOGY. For Professor Huber, Rektor of the Friedrich Wilhelms Universität, Bonn.

DESCRIPTION. Skull anterior to orbit. Snout low, broad; premaxillary alveoli circular, 4th largest, 5 in juvenile, with 2nd alveolus reduced and almost lost, 4 in adult (2nd lost). Incisive foramen broad, tear-shaped; external nares apple-shaped, with a short anterior process of the premaxilla and nasals on its posterior margin. Deep reception pit for the first dentary tooth not reaching dorsal surface. Fourth dentary tooth reception notch prominent, with a secondary pit medial to it on the palate. Premaxillary-maxillary suture relatively straight, with a slight posterior convexity. Maxillary alveoli 14, arranged in a typically crocodyline enlargement sequence with the 5th largest, laterally compressed particu-

larly the posterior-most 5. Low alveolar process on the anterior 6 maxillary alveoli. Dentary tooth reception pits 5, well-developed, medial to the upper series, between 6th-11th alveoli. Anterior teeth moderately robust, ovate in cross section. Posterior teeth with low, rounded crowns. All teeth with distinct anterior and posterior carinae. Palatal fenestra extending anteriorly to between the 7th and 8th maxillary teeth; straight suture with the palatine forming a short palatal process reaching anteriorly to 6th alveolus. Broad shelf

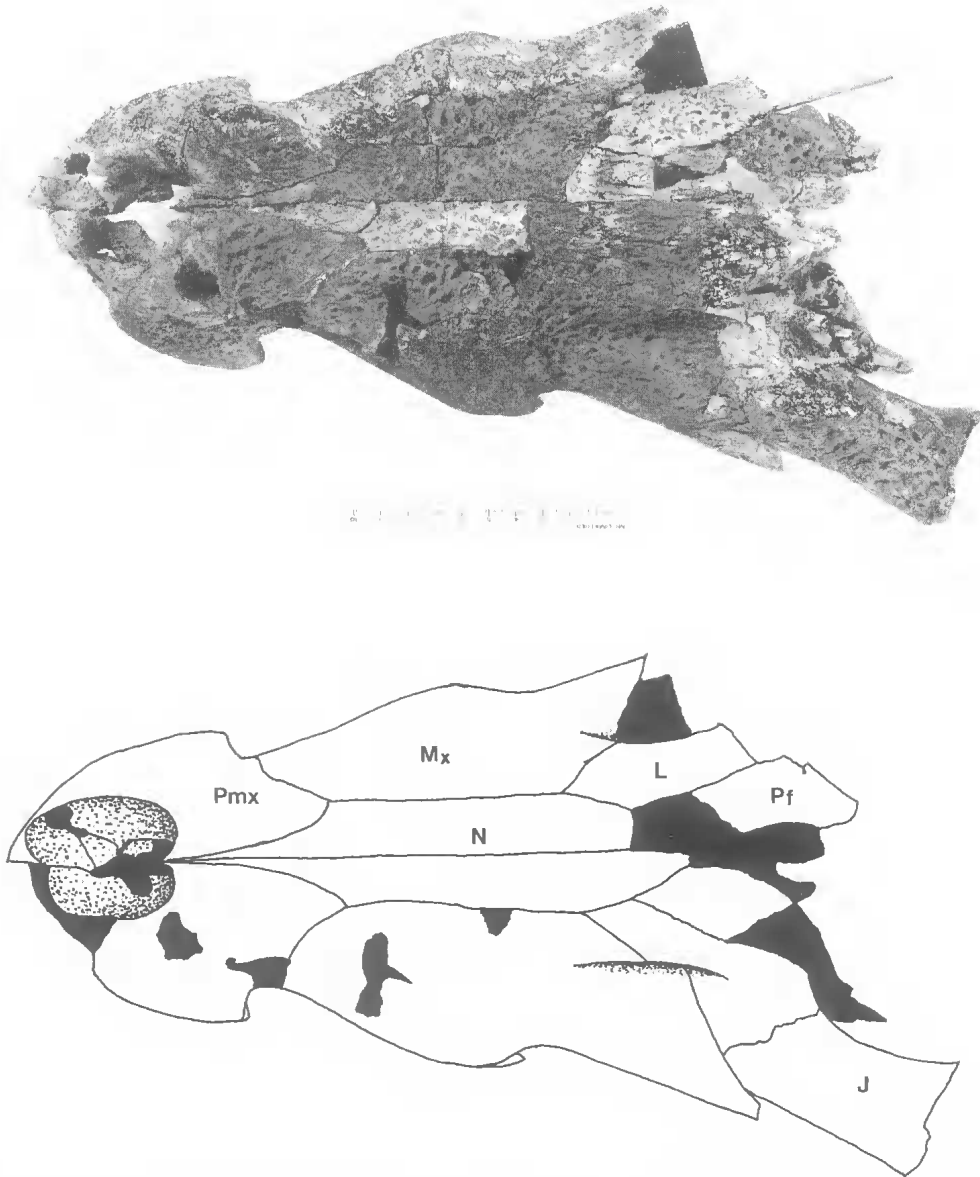


FIG. 12. *Baru wickeni*, QMF 16822, holotype, dorsal view, snout, with line interpretation. F=frontal; J=jugal; L=lacrimal; Mx=maxilla; N=nasal; Pf=prefrontal; Pmx=premaxilla. Scale in cm.

between palatal fenestra and posterior alveoli, rounded dorsally into the palatal fenestra and on to the internal surfaces of the maxilla. Sharp-crested ridge on the external surface of the maxilla at the line of the palate, starting above 10th alveolus, running off the posterior border of the maxilla.

Nasals broad, contacting the external nares, gradually widening to the lacrimal-maxilla-nasal triple junction, then tapering more sharply. Short, pointed anterior process of the frontals dividing the posterior extremities of the nasals. Lacrimals with low, rounded canthi rostrales, about twice the size of the prefrontals.

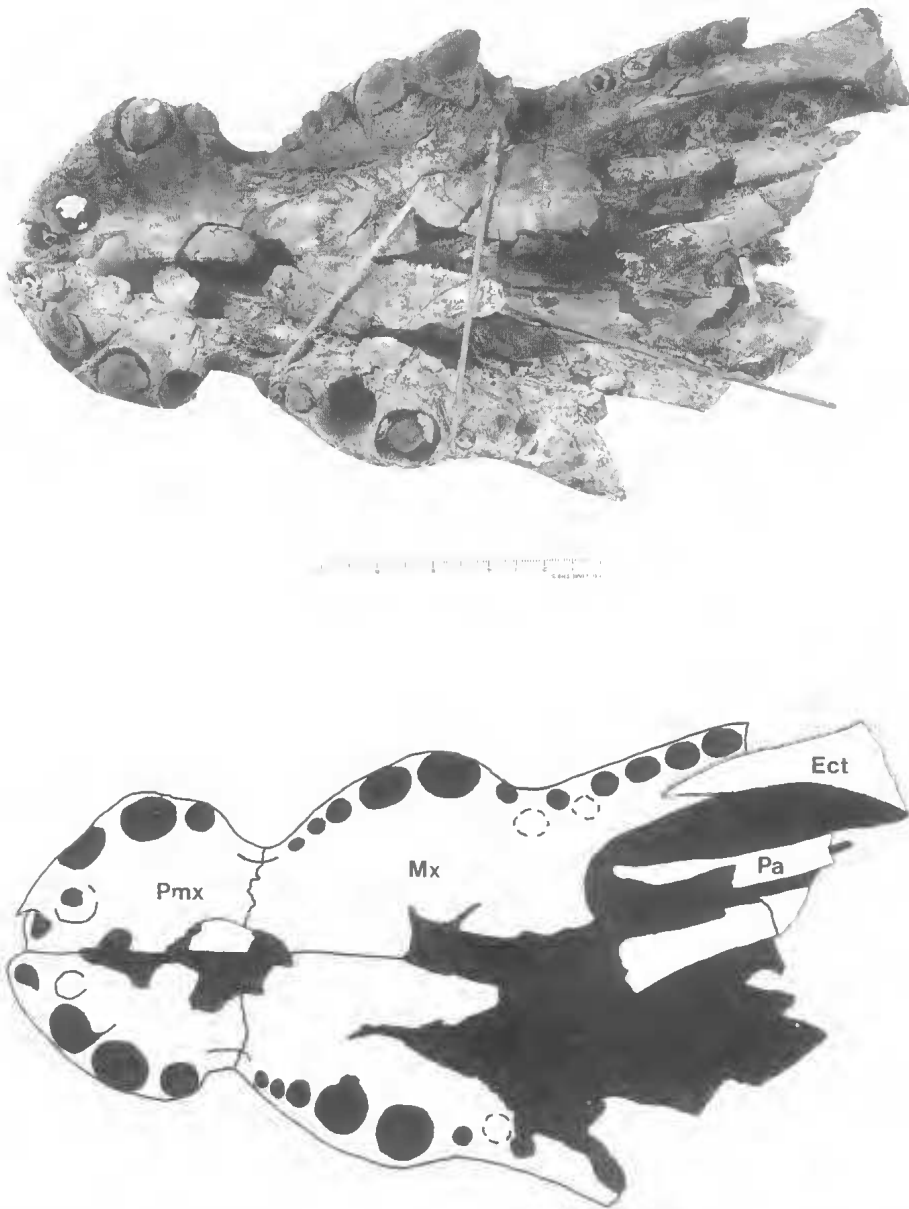


FIG. 13. *Baru wickeni*, QMF16822, holotype, snout, ventral view, with line interpretation. Ect=ectopterygoid; Mx=maxilla; Pa=palatine; Pmx=premaxilla. Scale in cm.

Dentary fragments. Dentary pseudoheterodont, with an undulating tooth row. Symphyseal region deeper and larger than in *Mekosuchus*. Dentary built up around the base of each alveolus, with this buttressing variable in proportion to size of the alveolus and not strongly developed. Slightly raised area on the dorsal surface medial to the 4th and 5th alveoli. Dorsal margin of dentary be-

tween and lateral to the 2nd and 3rd alveoli and between and lateral to the 7th, 8th and 9th alveoli with indentations for reception of teeth in the upper series, indicating that the upper series occluded lateral to the lower series. Splenial extending anteriorly to the 7th alveolus; symphysis extending to 5th alveolus. Sculpture of indistinct

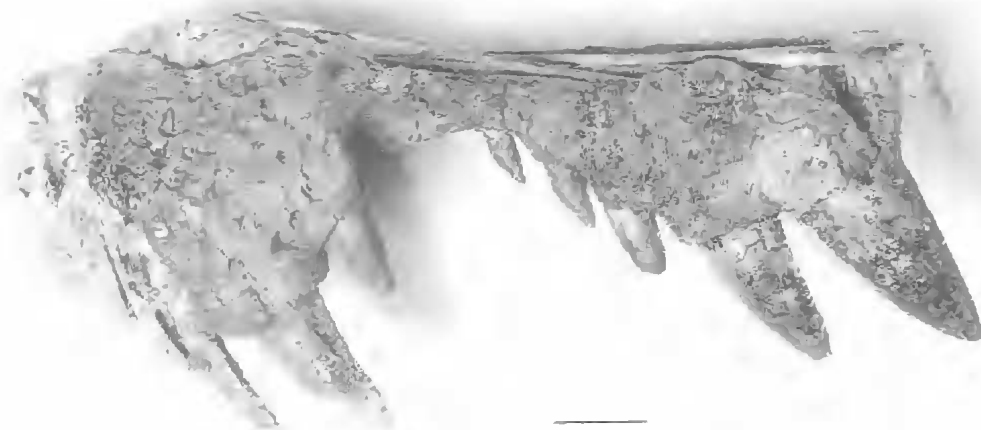


FIG. 14. *Baru wickeni*, QMF16822, holotype, partial left maxilla and premaxilla, lateral view. Scale = 2cm.

scarring on the ventral surfaces of the dentary merging to well developed pitting dorsally.

DISCUSSION. This mandible is assigned to *B. huberi* because it is the only unassigned mandible of appropriate proportions and size range from White Hunter Site. QMF31068 is an almost exact fit for QMF31060. The other 3 mandibular forms from White Hunter Site can be shown to belong to other taxa.

***Baru wickeni* sp. nov.**
(Figs 12-17)

MATERIAL. Holotype. QMF16822 (Figs 12-14) associated posterior cervical and lumbar vertebrae and a calcaneum. Paratypes QMF31070, anterior portions of mandibles; NTM P8738-1, posterior right skull fragment and associated right anterior dentary fragment; NTM P8681-14, left mandible lacking the articular and adjacent angular and surangular posterior to the lateral foramen and a small portion of the dentary at the level of the third tooth; NTM P8738-1, right jugal, pterygoid, ectopterygoid and posterior maxilla and an associated dentary fragment; QMF16823, jugal fragment; QMF16824, premaxillary fragments; QMF16825, right dentary; QMF16826, right dentary. All from Oligocene (System A) Site D, Riversleigh. QMF31071 and QMF31072, posterior portions of large mandibles and QMF31073, anterior dentary fragment. All from late Oligocene White Hunter Site, Riversleigh. SAMP27866, right premaxilla from late Oligocene Pancake Site, Riversleigh. QMF31074, right maxillary fragment and fragment of skull roof from late Oligocene Stieky Beak Site, Riversleigh.

ETYMOLOGY. For Tony Wicken, University of NSW, for supporting the Riversleigh Research Project.

DIAGNOSIS. Snout narrower than *B. huberi* or *B. darrowi*; deep; anteriorly pointed premaxillae; 13 maxillary teeth; nasals entering external nares; anterior termination of nasals long and thin, strongly constricted by premaxillae; non-serrated carinae; mandibular symphysis extending posteriorly to 6th or 7th dentary teeth.

DESCRIPTION. Skull material. Snout narrower than *B. darrowi* or *B. huberi*, similar in depth to *B. darrowi*. Premaxilla pointed anteriorly rather than rounded as in the other 2 species. Teeth similar to *B. darrowi*, lacking serrated carinae. Premaxillary alveoli in adults 4, in juveniles 5, with 2nd alveolus lost during growth. Maxillae with short posterior process medially invading lacrimal (not present in *B. darrowi* and unknown in *B. huberi*). Maxillary alveoli 13; palatal fenestra extending anteriorly to the level of 7th maxillary alveolus. Nasals entering premaxillae unlike *B. darrowi* but similarly to *B. huberi*. Anterior nasals distinctive in *B. wickeni*, being thin slivers strongly constricted between the premaxillae. Lacrimal with distinct, rounded *canthus rostralis*, extending for a short distance onto the maxilla. Jugal with well-defined, arched ridge on the exterior surface.

Mandibles. Alveoli 15, subcircular except for the 4 slightly laterally compressed most posterior. Alveoli 3rd-6th on an alveolar process most strongly developed around the 4th alveolus. No



FIG. 15. *Baru wickeni*, NTM P8738-1, portions of the right side of the skull with associated dentary fragment, lateral view. Scale = 2cm.

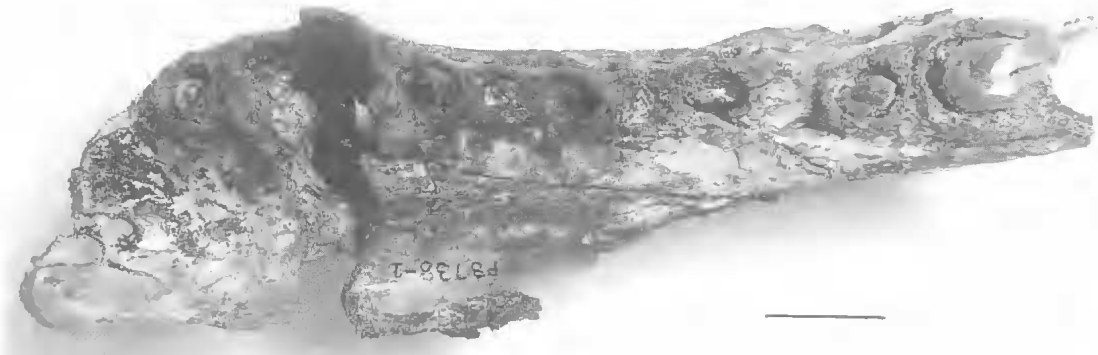


FIG. 16. *Baru wickeni*, NTM P8738-1, dentary fragment, dorsal view. Scale = 2cm.

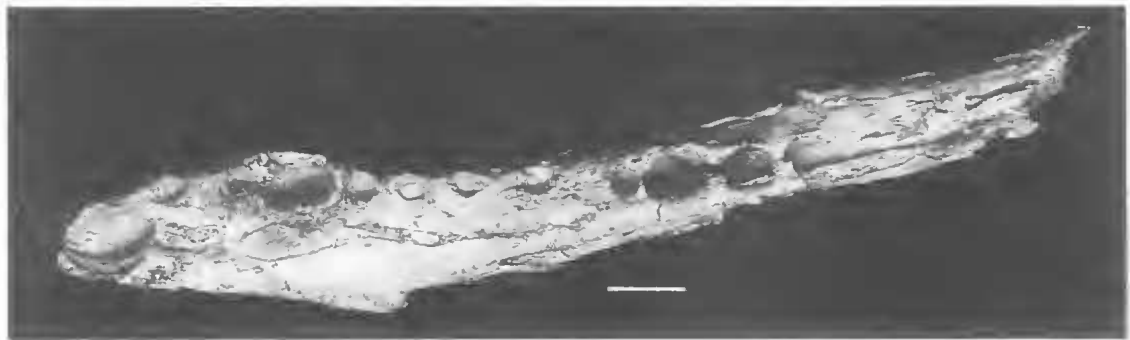


FIG. 17. *Baru wickeni*, QMF31070, dentary, dorsal view. Scale = 2cm.

reception pits for teeth from the upper series but spacings and a lateral sulcus between 2nd and 3rd alveoli, 7th and 8th alveoli and between the 8th and 9th alveoli. Symphyseal region narrow. Sym-

physis extending posteriorly to 6th alveolus; splenial reaching anteriorly to 7th.

External mandibular fenestrae ovate, of moderate size and inclined posteriorly. Surangular narrow dorsoventrally, inclined posteriorly with

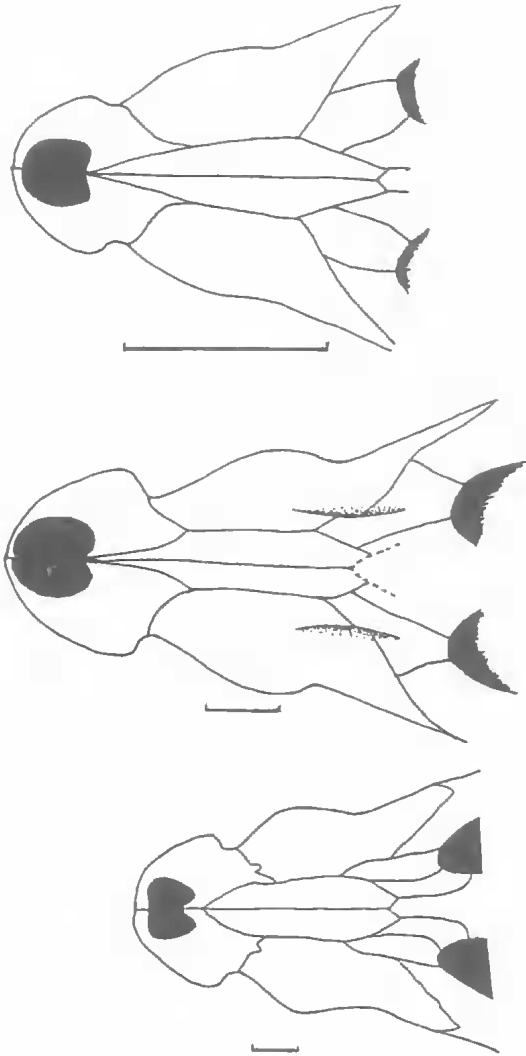


FIG. 18. Dorsal views of reconstructed snouts of *Baru huberi* (top), *B. wickeni* (middle) and *B. darrowi* (bottom) showing differences in sutural relations, particularly in the nasal-premaxillae sutures, and general proportions. *Baru huberi* based on QMF31060 (holotype), *B. wickeni* based on QMF16822 (holotype) and *B. darrowi* based on NTM P8695-8 (holotype). Scale = 5cm.

dorsal margin not parallel to the dentary. Angular slender, inclined. Smooth region for attachment of the posterior pterygoideus musculature sharply demarcated from the heavily sculptured areas of the angular and surangular by a low ridge. Articular and retroarticular process short, broad and steeply inclined.

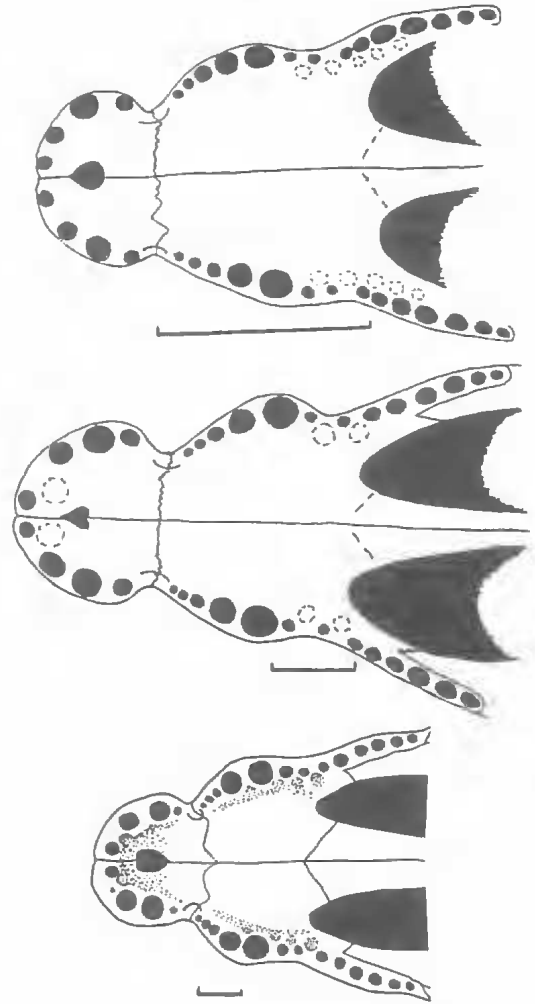


FIG. 19. Ventral views of reconstructed snouts of *Baru huberi* (top), *B. wickeni* (middle) and *B. darrowi* (bottom) showing differences in general proportions. *Baru huberi* based on QMF31060 (holotype), *B. wickeni* based on QMF16822 (holotype) and *B. darrowi* based on NTM P8695-8 (holotype). Scale = 5cm.

DISCUSSION. This new species is based primarily on material from Site D.

In describing *B. darrowi*, Willis et al. (1990) recognised that specimens from Bullock Creek differed from specimens from Riversleigh. However, at that stage there was insufficient material to separate 2 species. Since then a large portion of a snout from Riversleigh (part of QMF16822) a fragment of which was in the original description of *B. darrowi* has been rediscovered and

prepared. This and other new material allows the material from Riversleigh to be allocated to a third species of *Baru* (Figs 18, 19).

TWO CRANIAL FORMS

White Hunter Site has produced several posteriors of crocodylian skulls and skull decks representing 2 similar forms. No specimen duplicates portions of other specimens so although the cranial forms almost certainly pertain to 2 of the taxa described above, they cannot be assigned.

WHITE HUNTER CRANIAL FORM 1 (Figs 20-22)

MATERIAL. QMF31075, 31076 posterior of skulls; QMF31077, skull fragment; QMF31078, isolated parietal.

DIAGNOSIS. Supratemporal fenestrae tear-shaped with point directed anterolaterally and with posterior shelf formed by the squamosal; prominent expression of supraoccipital on skull deck; postorbital bar slender and round in section; postorbital-frontal suture twice the length of postorbital-parietal suture; foramen magnum wider than occipital condyle; width of supratemporal fenestrae greater than width of postorbital; sculpture of more or less regular pits closely spaced.

DESCRIPTION. Wide across the skull deck, high with the quadrate tucked under the squamosals. Supraoccipital prominent on the dorsal surface, forming a broad triangle almost excluding parietals from posterior margin of skull deck. Supratemporal fenestrae with an anterior point, teardrop-shaped, with much of the posterior and medial portions closed by a floor formed by the squamosal and parietals inside the supratemporal fenestrae. Posterior face of the skull with pronounced concavities on exoccipitals and squamosals for attachment of mandibular depressor muscles. Paroccipital process encroaching ventrally onto the quadrate. Foramen magnum subtriangular, wider than the occipital condyle. Basioccipital with pronounced keel ventral to the occipital condyle. Quadrates steeply inclined. Pterygoids forming large portion of the posterior margin of the palatal fenestrae; internal nares, although not preserved, must have been well to-

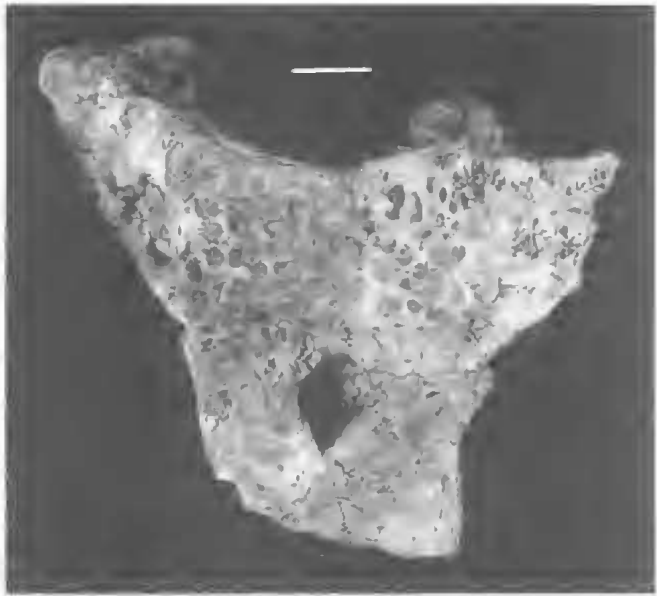


FIG. 20. Cranial form 1, QMF31075, posterior portion of skull, dorsal view. Scale = 1cm.

ward the posterior of the pterygoids. Otic meatus and foramina for the trigeminal nerve proportionally large. Laterosphenoids with a pronounced longitudinal crest medially on the ventral surface. Sculpture on the skull deck distinctive, deep and well-defined pits separated by equally distinct, uniform walls. Pits close spaced.

WHITE HUNTER CRANIAL FORM 2

MATERIAL. QMF31079, anterior fragment of skull deck; QMF31080, right postorbital.

DIAGNOSIS. Small supratemporal fenestrae laterally compressed, shallowly floored by squamosals; postorbital bars inset from skull deck margin, robust and triangular in section; postorbital-frontal suture equal in length to postorbital-parietal suture; width of postorbital greater than width of supratemporal fenestrae; sculpture of irregular shaped pits with irregular distribution.

DESCRIPTION. WH 2 is described where it differs from WH 1.

Supratemporal fenestrae narrower; squamosal flooring making supratemporal fenestrae shallower posteriorly. Sculpture pits on WH 2 are small and irregular, separated by thick, irregular walls. Sculptured skull deck overhanging postorbital bar on WH 2 but in WH 1 postorbital bar

marginal. Postorbital bar moderately robust, with triangular cross section. Postorbital very large compared to the supratemporal fenestrae. Triple junction between the postorbital, frontal and parietal distant from margins of supratemporal fenestrae.

DISCUSSION. The frontals associated with QMF31076 are very different from those referred to *Mekosuchus* (QMF31052) in being narrower and flat between the orbits. They are also deeper and have better defined *crania cristatae frontalis* than QMF31052. Thus cranial form 1 can be confidently excluded from *Mekosuchus* (but not *Baru* or *Quinkana*).

Although there are no frontals unambiguously associated with cranial form 2, the difference in sculpture (compared with QMF31052) and the thickness of the orbit margins of the postorbital make it unlikely that this cranial form represents *Mekosuchus*.

PALAEOECOLOGY

Four crocodylians have not previously been found in a single fauna in Australia. However, compared with world faunas, this is not an unusually high diversity of crocodylians, particularly when the 4 species have differing head shapes or when the site perhaps represents a thanatocenosis collected from 2 or more habitats.

Among extant crocodylians, many species have ranges that overlap but true sympatry is not common. In parts of South America 5 or 6 crocodylian ranges overlap but rarely do 3 or more share the same habitat (Gorzula, 1987; Magnusson & Lima, 1991). The range of *Crocodylus porosus* encompasses the ranges of *C. johnstoni*, *C. novae-guineae*, *C. mindorensis*, *C. siamensis*, *Tomistoma schlegelii* and parts of the range of *C. palustris* and *Gavialis gangeticus* (Ross & Magnusson, 1989; Groombridge, 1987) but rarely do any of these species exist in true sympatry. Where *C. porosus* and *C. johnstoni* have been found in sympatry the larger *C. porosus* tends to exclude *C. johnstoni* to the margins of the habitat or

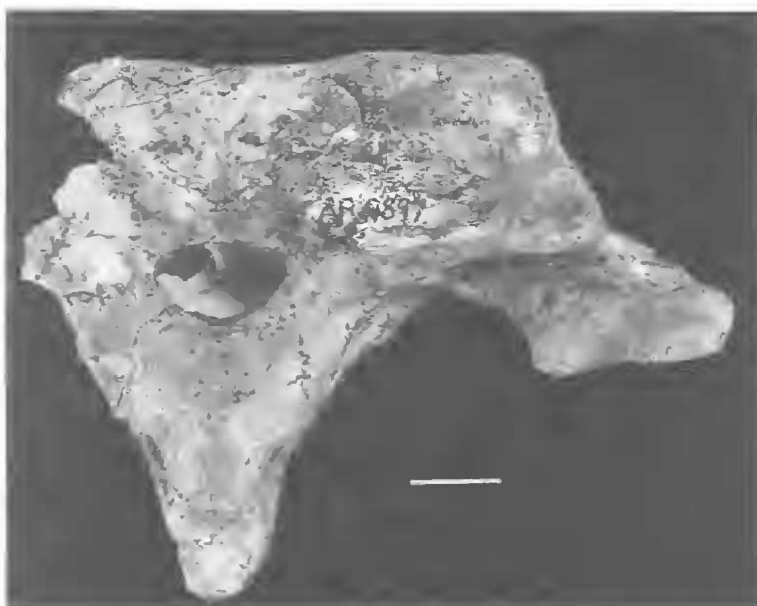


FIG. 21. Cranial form 1, QMF31075, posterior portion of skull, posterior view. Scale = 1cm.

sympatry is restricted by the need for different nesting substrates (Webb et al., 1983).

Modern studies of crocodylians in the Amazon Basin indicate that larger watercourses are occupied by larger, generalised crocodylians such as *Melanosuchus niger* and *Caiman crocodylus* as well as *Paleosuchus palpebrosus*, while smaller watercourses in closed canopy forests are occupied only by the more derived, deep-headed *P. trigonatus* (Magnusson, 1987, Magnusson & Lima, 1991). This could suggest that the variety of crocodylian head shapes at White Hunter Site is the result of a thanatocenosis collected from 2 or more different habitats.

Theoretically, 2 crocodylians may live sympatrically when there are differences in head shape (implying exploitation of different prey) or where small, broad-snouted species can evade larger broad-snouted species by escaping to marginal habitats (Meyer, 1984). In no extant crocodylian fauna, do 2 species share the same head shape (Meyer, 1984).

The most diverse fossil crocodylian fauna is from the La Venta fauna in Colombia which consisted of 8 species (4 broad-snouted, 1 duck-bill, 2 narrow-snouted and 1 ziphodont; Langston, 1965). However, that fauna is a thanatocenosis from over 240m stratigraphically. Sympatry was not demonstrated.

The Messel fauna of Germany is more likely a biocenosis and has 6 crocodylian species including large and small broad-snouted forms, a short-snouted form and two ziphodonts. A similar assemblage has been recovered from Gersaltal (Kuhn, 1938; Haubold, 1983; Haubold & Krumhiegel, 1984).

There are two possible explanations for the diversity of crocodylians in White Hunter Site. *Baru wickeni* is a large broad-snouted form while *B. huberi* is a much smaller broad-snouted form; *Mekosuchus whitehunterensis* is a small, short-snouted form; and *Quinkana meboldi* is a ziphodont. Compared to other fossil sites around the world and to modern analogues, the White Hunter assemblage differ enough to be sympatric exploiting different niches. Alternatively, they may indicate a thanatocenosis from two or more different habitats.

Arrangements of differing ecomorphs of groups of mammals from sites at Riversleigh support the hypothesis that these faunas represent biocenoses. A complex fauna of 8 species of bandicoots, belonging to clearly defined guilds, has been recovered from Upper Site (J. Muirhead, pers. comm.). Similarly, several species of ring-tail possums of differing ecomorphs have also been found in many sites at Riversleigh (M. Archer, pers. comm.). This pattern is apparently repeated in several other groups of mammals currently being investigated. That the Riversleigh mammalian faunas repeatedly show sympatry between several closely related taxa supports the hypothesis that Riversleigh sites preserve biocenoses rather than thanatocenoses. This supports the hypothesis that the White Hunter crocodylians were also sympatric.

CONCLUSIONS

The 4 crocodylians from White Hunter Site include the first record of *Mekosuchus* outside New Caledonia and demonstrates a surprising morphological diversity suggesting significant

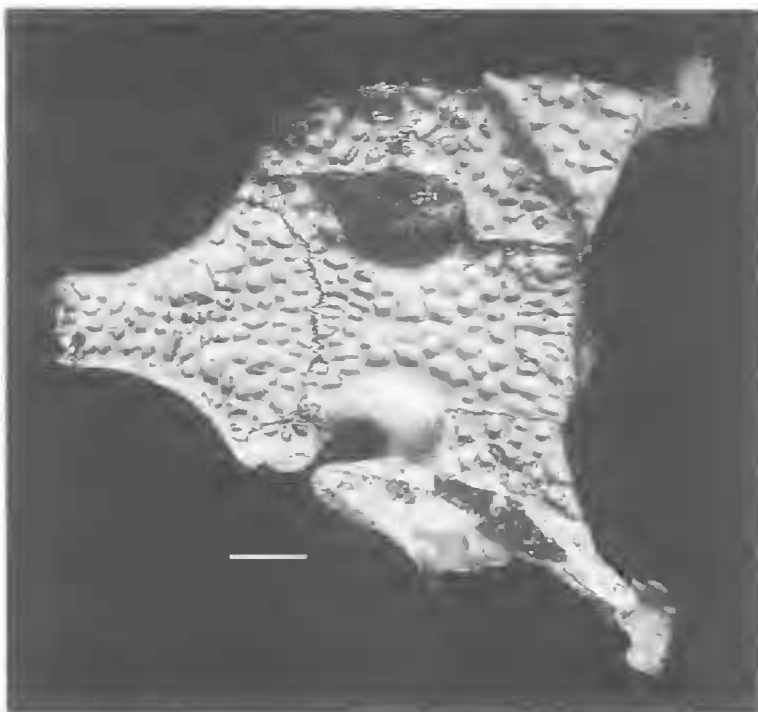


FIG. 22. Cranial form 1, QMF31076, posterior portion of skull, dorsal view. Scale = 1cm.

niche separation. This is the first record of such a diverse crocodylian fauna from Australia but it is consistent with the structure and complexity of crocodylian faunas known from elsewhere. By comparison with other Riversleigh faunas the crocodylian fauna of White Hunter Site was probably typical for Oligo-Miocene Australia.

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